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THE PHYTOGEOGRAPHY OF MEMBERS
OF PROTEACEAE IN AFRICA.

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INTRODUCTION.

South Africa occupies a unique position among the land masses of the southern hemisphere, for although some of its floras are as distinctively austral as are those of South America and Australasia, yet clues to past migrations into Africa from any lands in the south are lacking. In both the other southern continents there is evidence to show that even if elements of their floras did not originate in Antarctica, yet there must have been some transantarctic connection to show the close relationships that exist between certain components of their floras. Goodspeed in his comprehensive study of *Nicotiana*⁴ has shown this clearly and the distribution of other genera such as *Nothofagus*, *Hebe*, *Lomatia*, *Araucaria* etc. are best explained by some connection in the past between South America, Antarctica and Australasia. If South Africa received part of its present floras from the south, we might expect to find traces on islands such as Kerguelen, Marion and Heard. This is not the case for the floras of these islands show a definite affinity with that of South America although geographically they are much closer to Africa.

The problems of plant distribution in the southern hemisphere have long attracted attention. J. D. Hooker was a pioneer in this field⁵ and his discussions may still be read with profit. He clearly favoured the hypothesis of a southern origin though he was careful to state that there was no conclusive evidence available in support of it. Many others have followed his lead, among them the late Field Marshal Smuts¹¹, and to-day there are still many adherents of the so-called antarctic hypothesis. The

family Proteaceae looms large in any discussion on southern origins for the bulk of its members occur south of the equator. As recently as 1953 Good, referring to this family, states that they show "almost indisputable evidence of a southern origin"³. The African Proteaceae show a clear though rather remote affinity with those of Australia and this has often been used in arguments in favour of a common southern origin for both floras.

The object of the present paper is to record some facts of distribution of the family in Africa and to draw such conclusions as are legitimate.

AFRICAN MEMBERS OF PROTEACEAE AND THEIR DISTRIBUTION.

Proteaceae is divided into two subfamilies, Persoonioideae and Grevilleoideae. In South America all genera belong to Grevilleoideae. In Australia both subfamilies are represented. Hitherto all the South African genera have been placed in Persoonioideae but it will be shown later in this paper that one of them, *Brabeium*, has considerable claims to be regarded as a member of Grevilleoideae.

Fourteen genera occur in Africa. Two of them, *Protea* and *Faurea*, have a wide distribution, some of them extending north of the equator. A third, *Leucospermum*, has a much more restricted geographical range, but it too extends beyond the area of the Cape Flora. The remaining eleven genera are massed in the south western corner of Africa and are confined to the area characterised by the Cape flora.

With the exception of *Faurea* the distribution pattern of the genera within the Cape region is in no way different from that of other members of this most interesting flora. The significance of the distribution of species within the Cape area has been dealt with in recent papers (^{5,6,7}). All that is necessary here is to draw attention to certain salient facts. The mountain ranges in the southern tip of Africa run roughly parallel to the coast line. In the region now occupied by the Cape flora they were in existence by the end of the Triassic and since then their vegetation has suffered no major catastrophe. This holds true for the mountains only, for on the seaward side there have been marine invasions, while inland, evidence of arid periods is clearly indicated. Thus the only place where old types of vegetation will have found refuge is on the mountain ranges. Thus for our present purpose studies of distribution on the mountains are likely to produce results lacking elsewhere. Up to the present South Africa has not been divided into small phytogeographical units suitable for plotting the distribution of species. Use therefore has to be made of the established magisterial divisions, those for the south western Cape Province being shown in Fig. 1. The shaded divisions are those in which

the main mountain ranges occur and they are used in the tables which follow. In three cases where divisions are rather small, two have been united. In the west the rain falls mostly during the winter but the divisions from Swellendam eastwards show a gradual transition from winter to summer rainfall. Riversdale, the most easterly division selected, has its rainfall distributed fairly evenly throughout the year. The highest rainfall is in the Paarl, Stellenbosch and Caledon divisions.



FIG. 1.—Map of the south western Cape Province showing the divisional boundaries. The shaded divisions are those in which the main mountain ranges occur.

TABLE 1.—DISTRIBUTION OF SPECIES IN THREE OF THE CHARACTERISTIC FAMILIES OF THE CAPE FLORA.

	<i>Restionaceae</i>	<i>Burmanniaceae</i>	<i>Proteaceae</i>
Clanwilliam	44	14	68
Ceres	57	15	80
Worcester and Tulbagh	81	20	84
Paarl and Stellenbosch	83	23	97
Caledon	103	42	135
Swellendam	22	10	48
Heidelberg and Riversdale	57	9	40

In table 1 the number of species occurring in the shaded divisions is shown for three typical Cape families. All three show the same distributional pattern viz. a concentration of species in the Caledon Division in the south western corner and a diminution both northwards and eastwards. Table 2 provides the same information for five of the larger genera in the Cape flora. The same features are evident, though in the case of *Agathosma* the region of highest concentration has shifted northwards. Table 3 shows similar figures for the eight Cape species of *Proteaceae* containing 12 or more species. The information given here is

TABLE 2—DISTRIBUTION OF SPECIES IN FIVE CHARACTERISTIC CAPE GENERA.

	<i>Erica</i>	<i>Cliffortia</i>	<i>Phyllica</i>	<i>Muraltia</i>	<i>Agathosma</i>
Clanwilliam	74	10	29	12	39
Ceres	88	12	22	14	27
Worcester and Tulbagh ..	119	22	22	17	24
Paarl and Stellenbosch ..	144	33	18	27	16
Caledon	238	40	35	34	22
Swellendam	86	18	11	19	16
Heidelberg and Riversdale	74	15	17	16	18

TABLE 3—DISTRIBUTION OF SPECIES IN EIGHT GENERA OF *PROTEACEAE*.

	<i>Protea</i>	<i>Leucospermum</i>	<i>Leuca-dendron</i>	<i>Serruria</i>	<i>Spatalla</i>	<i>Sorocephalus</i>	<i>Paranomus</i>	<i>Mimetes</i>
Clanwilliam	19	10	20	8	2	3	2	0
Ceres	25	7	21	7	4	5	3	1
Worcester and Tulbagh ..	28	9	21	6	3	4	6	1
Paarl and Stellenbosch ..	27	9	21	13	8	3	3	5
Caledon	39	17	29	12	11	5	3	10
Swellendam	16	5	13	2	3	2	2	3
Heidelberg and Riversdale ..	14	6	9	1	3	0	2	2

based on records given in the *Flora Capensis*, supplemented by subsequent records in the Bolus Herbarium and in the herbarium of the department of Botany in the University of Cape Town. The information is incomplete for it has become clear that much more work on this family is needed, but it is sufficiently accurate to demonstrate that *Proteaceous* genera show a distributional pattern similar in all respects to those of other components of the Cape flora.

Leucospermum has the most restricted range of the three genera extending outside the Cape area. One species occurs on mountains in Namaqualand but there have been no records of any species in either South West Africa or Angola. In the east the genus extends further to the north but has not been recorded beyond Rhodesia and Mozambique. The two remaining genera have a much wider distribution and will be considered separately.

Protea is the largest genus and has over 90 species in Temperate South Africa. These, as we have seen, show a concentration of species in the south west but species occur outside the Cape area on high ground in the east. In Tropical Africa there are over 50 species. A comparison between the Cape and the non-Cape species brings to light a significant fact. Among the Cape species the three with the widest range extend from the Clanwilliam to the Albany Divisions. These are *P. mellifera*, *P. grandiflora* and *P. cynaroides*. They are liable to be found throughout their range wherever a suitable habitat occurs. In other words they show a continuous type of distribution over a somewhat limited area when we are considering Africa as a whole. The Cape area is shaded in the map given in Fig. 2.

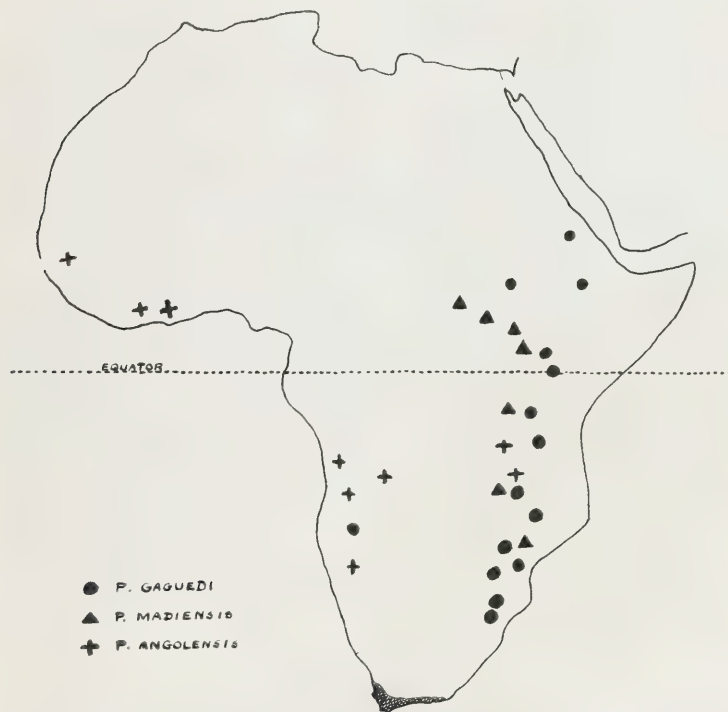


FIG. 2—Outline map of Africa showing the distribution of three species of *Protea*. The area characterised by the Cape flora is shaded.

On the other hand many of the non-Cape species show not only a very wide type of distribution but also marked discontinuities. This is illus-

trated in Fig. 2 where the distribution of three such species is shown. They are *P. gagedi* (syn. *P. abyssinica*), *P. angolensis* and *P. madiensis*. *P. gagedi* has the widest range of all. It is largely an eastern species, occurring on mountains and higher ground from Eritrea north of the equator to the Transvaal in the south. It has also been recorded from Angola. A glance at the map will show how widely separated the localities are from which this species has been recorded. *P. angolensis* shows similar features but its territory is largely western. Its most northerly station is in French Guinea and its most southerly in South West Africa. It has outliers in the east in Tanganyika and Nyasaland. The third example, *P. madiensis*, has a less spectacular range but here too discontinuities are marked.

Discontinuities in distribution such as are found in Central Africa can hardly be explained otherwise than by assuming that the species must at one time have had a more continuous range and that the isolated stations of to-day indicate that such species are relics. In the Cape area there are no marked discontinuities and few of the species extend even a short distance out of the Cape region. On the other hand many species of the south occupy very limited areas and are likely to be youthful endemics. Thus the facts of distribution suggest that the older species of *Protea* are those of Central Africa and that therefore *Protea* does not support the theory of a southern origin.

Faurea is a smaller genus than *Protea* having only seventeen species but in many respects its distribution affords a parallel to that of *Protea*. A species *F. rochetiana* (syn. *Leucospermum rochetianum*) occurs as far north as Abyssinia. The genus has the same widely spread, discontinuous species in Central Africa. Such are *F. saligna* which extends from Uganda and Tropical West Africa in the north to the Transvaal and Natal in the south, and *F. speciosa* with a similar range. However, there are two geographical features which distinguish *Faurea* from other African *Proteaceae*. It is not confined to the mainland but extends to Madagascar where one species occurs. The second feature is that no species of the genus is a member of the Cape flora. The most southerly species, *F. macnaughtoni* occurs at Knysna but it is a forest tree and never enters into the composition of the Cape sclerophyll.

FOSSIL EVIDENCE.

Simpson working on lignites on the west coast of Scotland, made some interesting discoveries which have been recorded in the second edition of Walton's Fossil Plants¹². The older (the Ardnamurchan beds) are presumably of Oligocene age and contain among other pollen grains those of the proteaceous genera, *Faurea*, *Lambertia* and *Petrophila*. The other

series (the Mull beds) are either of late Miocene or Pliocene age. In these proteaceous pollen is again found but in this case *Dryandra* replaces *Faurea*. To-day *Faurea* occurs only in Africa and Madagascar while the other genera are in Australia. This is clear evidence that in Tertiary times Proteaceae occurred in northern Europe. The fact that Proteaceae also occurred in North America at the same time is provided by the work of MacGinitie working on the Florissant Beds of Colorado. He found foliage and fruit of a species of *Lomatia*, *L. lineata*, allied to *L. ferruginea* which grows in South America to-day. At the present time there are three species of *Lomatia* in Chile, two in Tasmania and four in Australia.

THE TAXONOMIC POSITION OF *Brabeium*.

Brabeium, with a single species *B. stellatifolium*, is confined to the Cape region, occurring along streamsides and in other damp but not shaded places. All other African Proteaceae are clearly related to one another but *Brabeium* differs in almost every respect. Hitherto it has been placed in the subfamily Persoonioideae, tribe Persoonieae, but if we do not rely exclusively on the fruit for determining its true affinities, it fits better into the subfamily Grevilleoideae. Mr S. Garside, who for many years has made a special study of the family Proteaceae, has come independently to the same conclusion. The features that distinguish it from the other African genera are its whorled leaves, the deciduous bracts with more than one flower in each axil, the cup-like growth round the base of the ovary in place of separate scales, the free stamens and the ovary with two pendulous ovules. True it lacks the follicular fruit of most of the Grevilleoideae but the Australian genus *Macadamia*, placed in this subfamily, also has an indehiscent fruit. Indeed Bentham and Hooker record in the *Genera Plantarum*¹ that *Macadamia verticillata* is very similar to the Cape *Brabeium stellatifolium*. Whorled leaves are not common in Proteaceae and it is tempting to speculate that the ancestor of both these may have been *Lambertia* which has leaves of this kind. The records of pollen of *Lambertia* in Scotland during the Tertiary period are suggestive. However the mystery still remains of how this aberrant member of Proteaceae in Africa came to be isolated in the extreme south.

It is interesting to note that *Brabeium* has seven as its basic number of chromosomes². This number though recorded for several Australian genera, is unknown among the other African genera where twelve is the most characteristic basic number. A record of chromosome numbers in *Faurea* appears to be lacking and it would be of great interest to obtain chromosome counts in this, apparently the most ancient of our African genera.

CONCLUSIONS.

The fact that the bulk of the Proteaceae in Africa are massed in the south western corner, has long been known. It has been shown in this paper that their distribution within this area follows the typical pattern of any true member of the Cape flora, that is, they are concentrated in the south west and their numbers diminish in an orderly fashion both northwards and eastwards. The author has on previous occasions given reasons for thinking that this phenomenon is due to secondary causes which have operated in relatively recent times.

In considering the distribution of Proteaceae in Africa it is most striking that in the area of greatest concentration there are no marked discontinuities. Further the numbers of closely related species occupying limited and adjacent or overlapping areas is another noteworthy feature. Turning to distribution in Central Africa, there the picture is very different. The widespread species exhibit discontinuities of a most impressive kind. If the family had had a southern origin, then surely the reverse would have been the case?

Proteaceous fossils have long been suspected in Cretaceous and Tertiary rocks but their identifications have been open to doubt. However, we find a scientist as cautious as the late Sir Albert Seward expressing the belief that some of the identifications would prove to be correct¹⁰. Recent work to which reference has been made, makes it certain that Proteaceae were in existence in the Northern Hemisphere in Tertiary times. If we add to this the facts of present-day distribution in Africa, then the hypothesis of a northern origin has much to commend it.

It is well known that since mid-Tertiary times the floras of the Northern Hemisphere have undergone profound changes. An analysis of Simpson's list of angiospermous and gymnospermous pollen grains from the Scottish lignites¹², showing where the same genera are to be found to-day, is of interest in the study of plant migrations.

	<i>Ardnamurchan Beds</i>			<i>Mull Beds</i>		
	(19 genera)			(30 genera)		
Europe	..	..	2	..	..	11
America	..	..	4	..	..	14
Asia	..	..	11	..	..	23
Africa	..	..	3	..	..	3
Australasia ..	..	..	7	..	..	7

These figures show that the main paths of migration were mainly east and west. However, some genera found their way into Africa and Australia. The barrier to southward migration seems to have been stronger in Africa than Australia but this is hardly surprising. The Tethys Sea must have been a formidable obstacle to movements into Africa and

at times desert conditions must have imposed yet another barrier. However it seems clear that there were periods when the routes to the south must have been open and it is likely that at such times the Proteaceae made their way into Africa.

SUMMARY.

The Proteaceae have at times been used to support the southern origin of some austral floras. Thirteen of the fourteen African genera have a high concentration of species in the winter rainfall area. Protea has a wide distribution in Tropical Africa with marked discontinuities. Faurea, the only non-Cape genus, has a range in Central Africa similar to that of Protea but is also found in Madagascar. Palynological evidence indicates that Faurea occurred in Scotland in mid-Tertiary times. Marked discontinuities in distribution in Central Africa and the absence of this phenomenon in the south support the northern origin of the family. The problem of Brabeium is discussed.

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